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NOTES ON GEOGRAPHIC DISTRIBUTION

Cnidaria, Scleractinia, Siderastreidae, *Siderastrea siderea* (Ellis and Solander, 1786): Hartt Expedition and the first record of a Caribbean siderastreid in tropical Southwestern Atlantic

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ABSTRACT: Samples of *Siderastrea* collected by the geologist C. F. Hartt during expedition to Brazil (19th century), and deposited at the National Museum of the Natural History, Smithsonian Institution, have been re-examined. Taxonomical analyses resulted in the identification of a colony of *S. siderea* from offshore northern Bahia state. Following recent studies, the occurrence of Caribbean siderastreids to western South Atlantic provides new criteria to assess intra- and interpopulational morphological variation of the endemic *S. stellata*, refuting historical trends of synonymizations possibly biased by long-term taxonomical misunderstandings.

After assisting Louis Agassiz in the Thayer Expedition to Brazil (1865-1866), the Canadian geologist Charles Frederic Hartt (1840-1878) returned several times and explored a vast area of the Brazilian coast (Freitas 2001). An enormous collection, and a number of papers and reports resulted from these scientific explorations. Samples of scleractinian corals from the 1867 Hartt Expedition to Abrolhos Reefs, southern Bahia, were deposited in the Museum of Yale College (Verrill 1868). Based on these specimens, Verrill (1868) described nine new species, including the endemic and highly variable *Siderastrea stellata*. Colonies of *Siderastrea* from the last of Hartt's journeys (1874-1876), covering the northeastern coast, were deposited at the National Museum of Natural History, Smithsonian Institution (Washington, DC). As part of a revision of the genus *Siderastrea* (see Neves 2004), this material has been re-examined. Based on skeletal attributes, one particular specimen from Hartt's collection previously identified only at genus level was attributed to *S. siderea*. This is the first reported occurrence of *S. siderea* from Brazil, where despite of the remarkable variation and number of morphotypes, the genus has been considered to be represented solely by *S. stellata* (see Laborel 1967; 1969/70; 1974). Indeed, this 'myth' has recently been rejected in thesis by Neves (unpublished data) and Neves *et al.* (2008) by determining the sympatric distribution of *S. radians* within *S. stellata* population, majorly along the northeastern section of the Brazilian coast. Therefore, besides introducing relevant changes to the geographical pattern of the genus *Siderastrea*, a group widely represented in shallow-water reef systems and coral communities, the occurrence of the Caribbean *S. siderea* in western South Atlantic provides further and reliable taxonomical criteria to assess intra- and interpopulational morphological variation of the endemic *S. stellata*.

Hartt's specimens deposited in the collections of the National Museum of Natural History (NMNH) were examined under a Wild M8® stereo microscope fitted with an ocular micrometer. A single small colony (USNM 10948) collected offshore northern Bahia state (12°48'00" S, 38°0'00" W), approximately 17 km from the coast, was identified as *S. siderea* (Figure 1). The analyses of corallite structures were primarily based on Foster (1979; 1980) and Budd and Guzmán (1994). For a consistent pattern of septal number and arrangement, only completely developed corallites were examined. For comparison purposes the following Atlantic specimens were also examined (*= species name redesignated/determined after analyses): ***S. siderea*** – USNM 36919 (Curaçao, 'Albatross'),

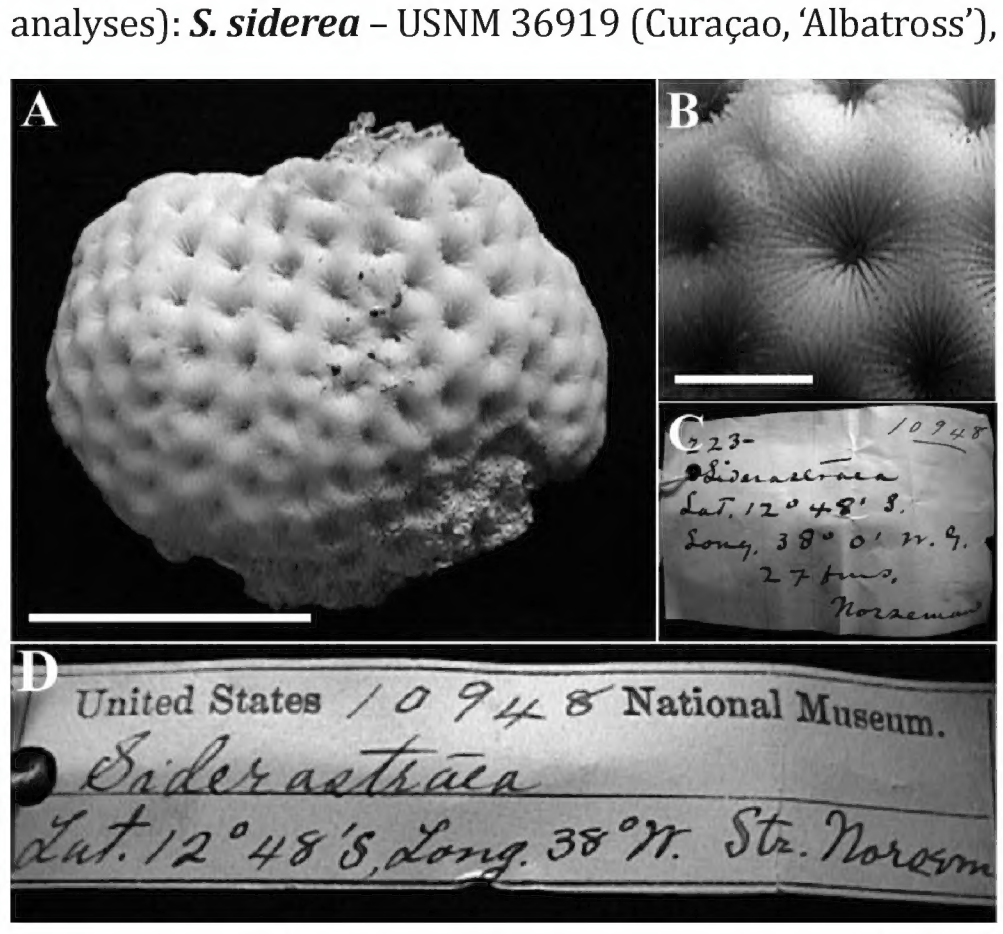

FIGURE 1. A) USNM 10948, specimen from Hartt's collection attributed to *S. siderea*. B) Detail of a completely developed corallite. C and D) Original labels found attached to the colony. Scale bars: A = 2 cm, B = 3 mm.

USNM 047607 (Belize), USNM 047611 (Belize), USNM 84238*(= *S. radians*, Brazil, 'Hartt Expedition'), USNM 90250 (Venezuela), USNM 93957 (San Blas Archipelago, Panama); ***S. radians*** - USNM 047605 (Belize), USNM 047610 (Belize), USNM 78220 (I. Ascension), USNM 78221 (I. Ascension), USNM 74961 (Belize), USNM 96369 (I. Ascension), USNM 96978 (I. Ascension), USNM 294338 (I. Ascension); ***S. stellata*** – USNM 83831* (= *S. radians*, Brazil, 'Hartt Expedition'), USNM 83832* (= *S. radians*, Jamaica), USNM 83833* (= *S. radians*, Brazil, 'Hartt Expedition'); *Siderastrea sp.* – USNM 10891* (= *S. radians*, Brazil, 'Hartt-Expedition'), USNM 10903* (= *S. radians*, Brazil, 'Hartt Expedition'), USNM 10932* (= *S. radians*, Brazil, 'Hartt Expedition'), USNM 10934* (= *S. radians*, Brazil, 'Hartt Expedition'), USNM 10937* (= *S. radians*, Brazil, 'Hartt Expedition'), USNM 10944* (= *S. stellata*, Brazil, 'Hartt Expedition'), USNM 10947* (= *S. radians*, Brazil, 'Hartt Expedition'), USNM 10978* (= *S. radians*, Brazil, 'Hartt Expedition'), USNM 10979* (= *S. stellata*, Brazil, 'Hartt Expedition'), USNM 10938* (= *S. radians*, Brazil, 'Hartt Expedition'), USNM 11003* (= *S. siderea*, West Indies, 'Albatross'), USNM 36872* (= *S. radians*, Bahamas, 'Albatross'), USNM 54232* (= *S. siderea*, Florida), USNM 83834* (= *S. radians*, Cape Verde), USNM 90174* (= *S. radians*, Bahamas, 'Anton Dohrn'), USNM 90175* (= *S. siderea*, Bahamas, 'Anton Dohrn'), USNM 90225* (= *S. siderea*, Florida), USNM 90249* (= *S. radians*, Venezuela), USNM 90254* (= *S. radians*, Cape Verde).
Acronym= United states National Museum/National Museum of Natural History

Family SIDERASTREIDAE Vaughan and Wells 1943
Astreidae. (*pars*) Milne Edwards and Haime (1949: 95); (*pars*) Milne Edwards and Haime (1850: 23)
Plesiofungidae. (*pars*) Gregory (1895: 277); (*pars*) Quelch (1886: 113)
Fungidae. (*pars*) Vaughan (1900: 154); (*pars*) Vaughan (1923: 175); (as Fungiidae, *pars*) Crossland (1948: 193)
Agaricidae. (*pars*) Gravier (1909: 17); (*pars*) Thiel (1928: 274); (as Agariciidae, n. sp.) Vaughan (1919: 425); (as Agariciidae, n. sp.) Wells (1933: 105)
Siderastreidae. (diag) Vaughan and Wells (1943: 125); (diag) Veron and Pichon (1979: 85)

Genus *Siderastrea* de Blainville 1830
Madrepora. (*pars*) Pallas (1766: 322)
Astrea. (*pars*) Lamarck (1801: 371); (as *Astraea*, *nom nud*) Milne Edwards (1857: 505); (as *Astraea*, *nom nud*) Gregory (1895: 278)
Siderastrea. (*pars*, diag) de Blainville (1830: 335); (diag) Milne Edwards and Haime (1949: 138); (diag) Milne Edwards and Haime (1850: 41); (diag) Vaughan (1919: 435); (diag) Sheppard and Sheppard (1991: 75)
Siderina. (*nom nud*) Dana (1846: 218)
Type-species: *Madrepora radians* Pallas, 1766

Siderastrea siderea (Ellis and Solander 1786)
Madrepora siderea. (diag) Ellis and Solander (1786: 168, pl 49, figs 1,2)
Astrea siderea. (n gen) Lamarck (1816: 267 - ed 2, p 417); (diag.) Milne Edwards (1857: 509, pl D7, fig 2)
Siderastrea siderea. (n gen, diag) de Blainville (1830: 335); (diag) Milne Edwards and Haime (1849: 141); (diag) Vaughan (1901: 309, pl 14, figs 1, 2, pl 16, fig 1); (biol) Duerden (1902: 588, pl 22-24, figs 150-160); (diag) Vaughan (1919: 443, pl 114, figs 2, 3, pl 122, figs 1, 2, 2a, 2b, 3, 3a); (diag) Squires (1958: 249, pl 35 fig 2, pl 36, fig 1); (diag) Budd and Guzmán (1994: 594, fig 4a); (as *Siderastraea siderea*, diag) Verrill (1901: 151, pl 30, fig 2,3)
Astrea trichophylla.(*syn*) Ehrenberg (1834: 95)
Pavonia siderea. (*syn*) Dana (1846: 331)
Siderastraea grandis. (*syn*) Duncan (1863: 441, pl 16, fig 5a,5b)

Description. The specimen examined is a small dry skeleton (4.0 x 3.0 cm) with a massive growth form development, encrusting base and distinct oval surface. Corallites cerioid (3.5 – 4.0 mm in diameter) with hexagonal appearance, each containing a deep columellar fossa (approximately 2.0 mm, from calicular edge to columella), theca prominent, numerous septa regularly distributed in four, sometimes five cycles, and an apparent double wall. The diagrams of Figure 2 represent the pattern of septal arrangement in four distinct corallites. Septal disposition follows hexameral symmetry, with a conspicuous fourth cycle (S4) ranging from 16 – 24 septa, and an incomplete fifth cycle (S5) with fewer elements. The presence of S5 is likely to occur independently of the full development of the fourth cycle (see Figure 2B). Septa are thin (S1 = 0.1 mm in width and 2.0 mm in length), crowded, bear dentate margins, and small spine-like prominences along lateral faces. The primary septa may develop 10 – 13 dentations, and the distal tooth often projects towards the solid columella fusing at its base, and contributing to its papillose aspect – columella usually has a central robust prominence which is surrounded by 3 or 6 smaller papillae derived from marginal teeth. Septal dentations are elongate, with finely serrate or eventually sharp top, and lateral cuspid-like projections; they are uniform in size (0.1 mm in width and 0.1 – 0.2 mm in height), and are distributed at regular intervals (distance between the teeth = 0.04 mm). The columella is small (0.8 mm in diameter, approximately), oval or relatively elongate. Synapticulae are arranged in four conspicuous rings (length of synapticulae at third ring = 0.07 mm, and distance between rings of synapticulae = 0.1 mm). The radial elements do not form a prominent septo-costa, although some contact is observed at the edges of neighboring marginal corallites, when the costae cross continuously the peritheca. Septa curving soft and gradually on theca, while descend vertically towards the columella. Fusion occurs between S2 – S3, S3 – S4, and S4 – S5, following a typical siderastreid pattern. Septa size: S1 ≥ S2 > S3 > S4 > S5. New corallites are produced exclusively by extratentacular budding.

Remarks. Diagnostic morphological skeletal traits to distinguish Atlantic siderastreids (information based on specimens analyzed at the NMNH and additional references) are provided in Table 1. Figure 3 shows the basic septal pattern of the three Atlantic species. Contrasting with *S. radians* and *S. stellata*, *S. siderea* does not undergo intratentacular budding. Consequently, among the Atlantic *Siderastrea* species, it has no tendency to develop meandroid corallites. Laborel (1974) suggested

an influence of the environment on the meandriform development of *Favia gravida* Verrill, 1868, but disregarded the effect of budding on corallite morphology. Despite the environmental gradient, the quite perfect polygonal corallites of *S. siderea* indicate extratentacular budding. Another peculiar characteristic of *S. siderea* is determined by its mode of sexual reproduction. The gonochoric *S. radians* and *S. stellata* are known to brood their embryos (Duerden 1904; Neves and da Silveira 2003), whereas the hermaphroditic *S. siderea* has been reported to shed gametes for external fertilization (Szmant 1986).

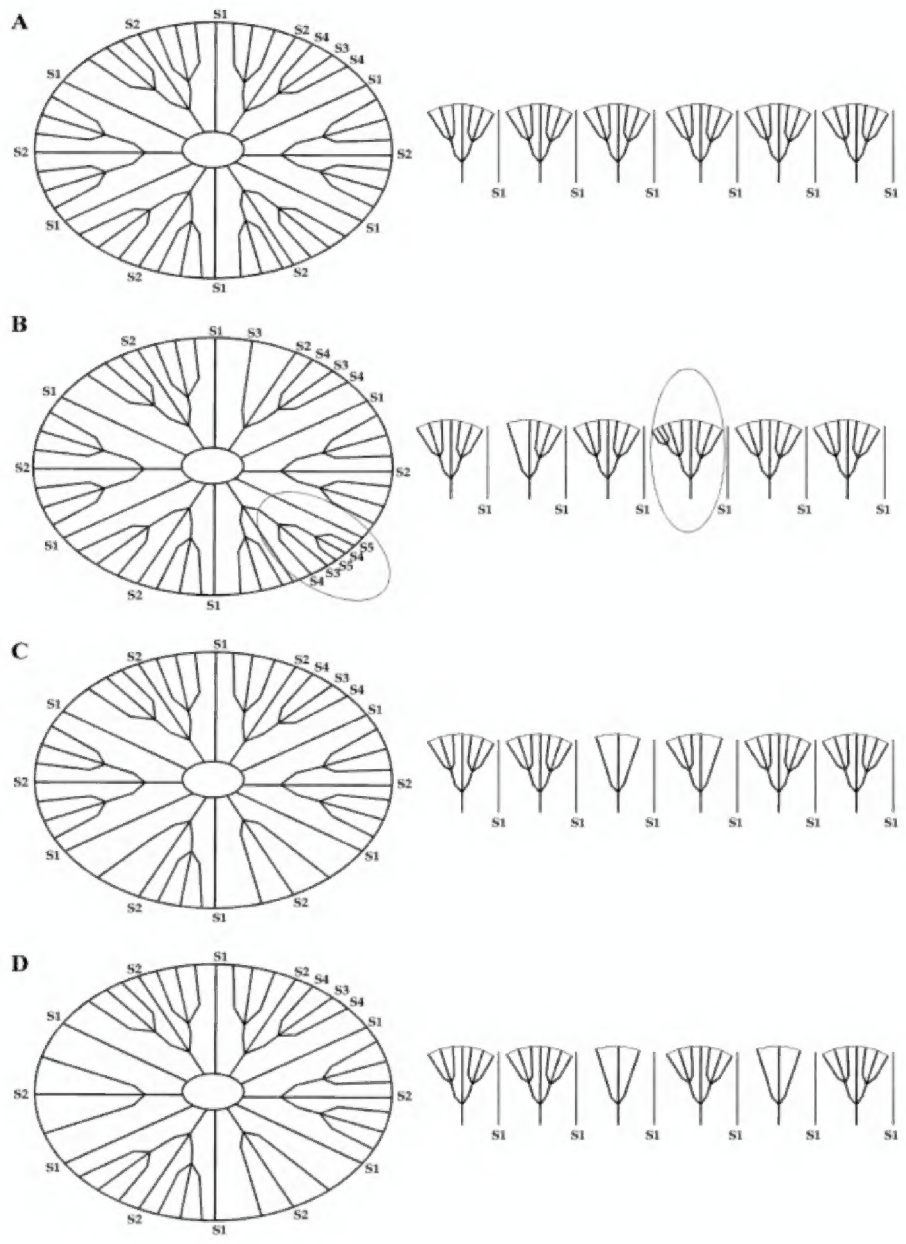

FIGURE 2. Diagrams of septa arrangement of four distinct corallites of the specimen analysed. A) Corallite with complete fourth cycle. B) Corallite with incomplete fourth and fifth cycles. Encircled, a sequence including S5 elements. C and D) Corallites with incomplete fourth cycle.

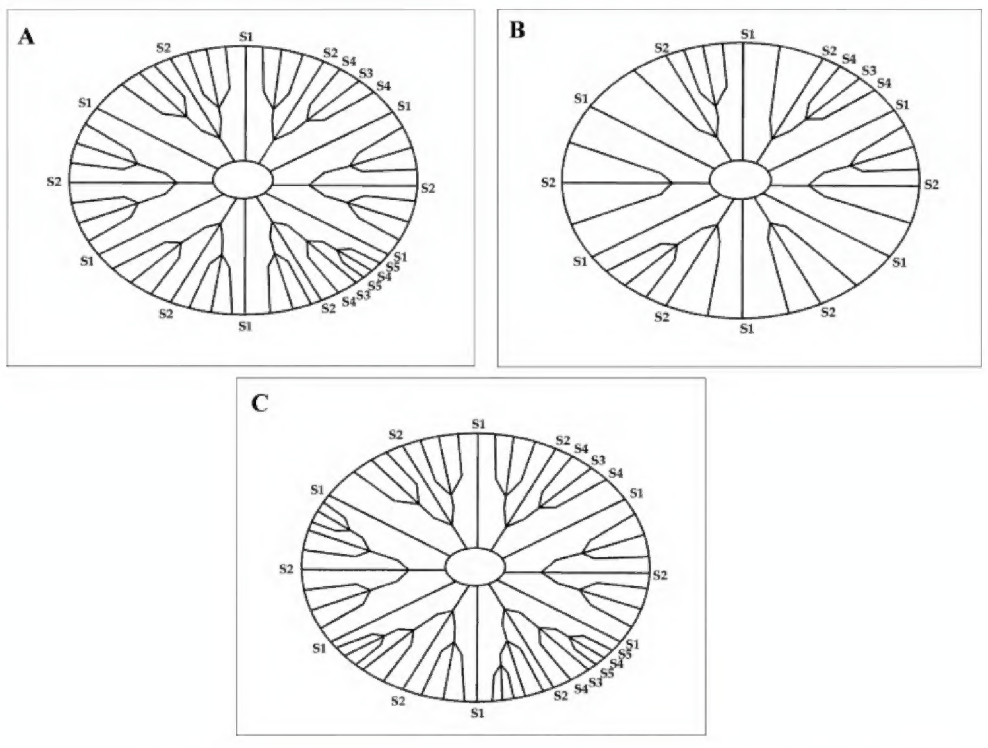

FIGURE 3. Basic septal pattern of Atlantic siderastreids. A) *S. stellata*. B) *S. radians*. C) *S. siderea*.

DISTRIBUTION. To the northern tropical Atlantic, Laborel (1974) suggested that *S. siderea* was endemic to the Caribbean region, while *S. radians* could be the dominant species to the west African coast (*e.g.* Cape Verde I.), being doubtful the status of the colonies with wide calices and numerous septa from the Gulf of Guinea (Figure 4). Although the identification is refuted by one of us (M. Pichon), Boshoff (1981) reported the presence of *S. siderea* in Mozambique (Inhaca Is.), West Indian Ocean, suggesting a wider distributional pattern. As its congener *S. radians*, *S. siderea* is found throughout the Caribbean Sea where it has been recorded in Jamaica (Goreau and Wells 1967), Puerto Rico (Almy Jr. and Carrión-Torres 1963), Lesser Antilles, in Curaçao (Debrot *et al.* 1998), St. Lucia (Fenner 1998), Barbados (Lewis 1997) and Trinidad (Kenny 1988), Venezuela, in the Gulf of Cariaco (Antonius 1980), Belize (Cairns 1982; Macintyre and Aronson 1997), Swan Is. (Tortora and Keith 1980), Costa Rica (Cortés 1997) and Panamá (Holst and Guzmán 1993; Clifton *et al.* 1996). Its range of occurrence also extends to the Gulf of Mexico, at East Flower Garden Banks (Bright *et al.* 1984) and northwards at Trysler Grounds/Big Rock (Schroeder and Hopkins 1997), Florida (Muthiga and Szmant 1987), and Bahamas, in the Turks and Caicos Is. (Chiappone *et al.* 1996). To the region of Abrolhos Archipelago (Southern Bahia state, Brazil), Laborel (1974) has specially pointed out to the variability of the endemic *S. stellata* with *radians*- and *siderea*-looking forms, but has not formally confirmed any of the Caribbean siderastreids to western South Atlantic.

The genus *Siderastrea* is represented by five nominal species: *S. radians* (Pallas, 1766); *S. siderea* (Ellis and Solander, 1786); *S. stellata* Verrill, 1868; *S. savignyana* Milne Edwards and Haime, 1850; and *S. glynni* Budd and Guzmán, 1994, all of them colonial and zooxanthellate (Budd and Guzmán 1994). The Atlantic *Siderastrea* complex includes the three former species, and the group has long puzzled taxonomists due to intraspecific morphological variability and interspecific overlapping of taxonomic characters. Hence, their specific status has been a constant subject of discussion and misunderstandings. For example, Yonge (1935) and Werner (unpublished data) referred to *S. stellata* as synonym of *S. radians*, while Laborel (1967) suggested *S. siderea* as an ecomorph of *S. radians*, and *S. stellata* as an archaic intermediary species. Similarly, Zlatarski and Estalella (1982) mentioned two forms of *S. radians* in Cuba but synonymized *S. siderea* as *S. radians*. However, as emphasized by Vaughan (1919), despite the similarities between the three Atlantic siderastreids, *S. stellata* is a very distinct species from both *S. siderea* and *S. radians*, which further differ from each other in a series of diagnostic characteristics, including depth of columellar fossa and structure of columella. Moreover, Budd (personal communication) pointed out that *S. radians* tends to develop into 'roller' forms, or spheroid unattached colonies, while *S. stellata* commonly shows a high incidence of meandroid or elliptical corallites. Another important divergence is related to the number and arrangement of septa. S. *radians* forms three complete cycles, and hardly presents elements of a fourth cycle (Verrill 1901; Vaughan 1919). On the other hand, *S. siderea* and *S. stellata* usually show a complete fourth cycle, and a

few elements of the fifth (Verrill 1901; Leão 1986).

Colonies of *S. siderea* are known to occur at highly variable depth and have been reported in waters deeper and cooler than the other two species (Bright *et al.* 1984; Schroeder and Hopkins 1997). The Amazon estuary is an important and effective barrier to Caribbean species, also inhibiting coral reef formation (Laborel 1967; Palacio 1982; Maida and Ferreira 1997). However, several planktonic forms, including larval stages, are known to flow through extensive areas of sediment and freshwater input (Scheltema 1986; Morgan 1995), corroborating the hypothesis that *S. siderea* seems to be resistant to turbulent and turbid environments (Jiménez and Cortés 1993). *Siderastrea siderea* is a broadcast-spawning species, and external fertilization is expected to enhance long-distance dispersal, promoting connection among populations (Jackson 1986). Also contributing to a high dispersal potential, free-swimming larvae have been predicted to delay metamorphosis until environmental cues indicate suitable habitats (Burke 1983). During their competency period, scleractinian larvae depend upon cilia for natatorial movement, but swimming speeds are extremely low (Harrison and Wallace 1990; Shanks 1995). As a result, the duration of the planktonic stage probably plays an

Table 1. Morphological characters of all Atlantic siderastreids. Modified from Budd and Guzmán (1994) and Werner (unpublished data), with additional information from: Milne Edwards and Haime (1849), Milne Edwards (1857), Verrill (1868, 1901), Vaughan (1919), Yonge (1935), Almy Jr. and Carrión-Torres (1963), Laborel (1969/70), Foster (1979, 1980), Debrot et al. (1998), and Neves (thesis, unpublished data). In parenthesis: maximum diameter of corallites, and minimum and maximum number of septa and synapticulae eventually observed. * Between pentagonal and hexagonal, often with an irregular development

Characters/Species	*S. stellata*	*S. radians*	*S. siderea*
Colony form	Rounded massive, or irregular encrusting	'Roller' form when unattached, irregular domes or encrusting	Dense skeleton, usually rounded massive, encrusting when young
Corallite development	Cerioid to subcerioid, pentagonal or hexagonal, feebly round, sometimes meandroid	Cerioid, subhexagonal*, marginal corallites eventually elongate	Cerioid, pentagonal or hexagonal, feebly round, no tendency to meandriform development
Calice diameter	2-5 (6) mm	2-3 (4) mm	3-5 (6) mm
Septa number per corallite	36 (34)-56 (58)	24-44 (46)	40-58 (64)
Septa arrangement	Hexameral plan, 3 complete cycles, 4th cycle complete or incomplete, 5th cycle incomplete or absent, 6th cycle rare	Hexameral plan, 3 complete cycles, 4th cycle always incomplete or absent, 5th cycle rare, 6th cycle absent	Hexameral plan, 3 complete cycles, 4th cycle rarely incomplete, 5th cycle incomplete or absent, 6th cycle rare
Septa thickness and slope	Thinner than *S. radians*, relatively regular in width and thickness, closely spaced, slope vertical towards the collumela, sometimes horizontal at marginal corallites	Unequal in width and thickness, larger and shorter than *S. stellata*, irregularly spaced, perpendicular to wall, descend vertically towards the columella	Slim, crowded, longer than *S. stellata* and *S. radians*, septa of the last cycle thinner, subacute at calice margin, slope vertical towards the columella
Columella structure	Papillose, sometimes feebly trabecular, oval or elongate, with 1-7 ornamented papillae	Larger than *S. stellata*, solid, smooth or with 1-3 fused papillae, occasionally fusion is reduced and about 5 short, flattened papillae are observed	Small, solid, usually oval with 1central pit or 3-6 smooth, or feebly ornamented papillae
Columellar fossa	Usually narrow, shallow, 1-2 mm depth	Wider than *S. stellata*, shallow, < 2 mm depth	Narrow, deep, 2–3 mm depth
Synapticulae	2(3)-4(5) irregular synapticular rings	2-4 irregular synapticular rings	4(3)-5(6) regular synapticular rings

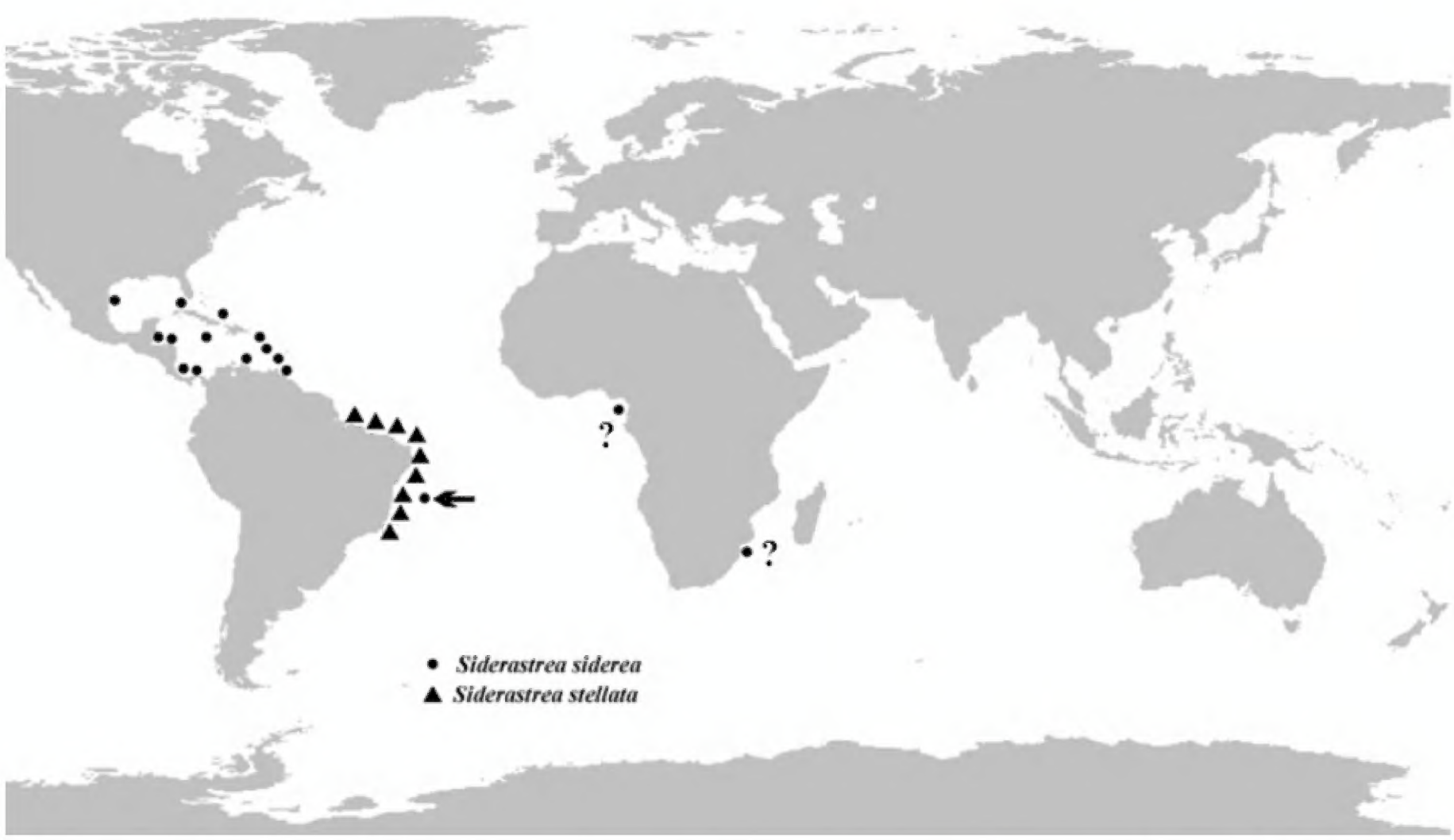

Figure 4. Map of distribution of *S. siderea* and *S. stellata*. Arrow is indicating the occurrence of *S. siderea* in Brazil. Following Laborel (1974) and Pichon (pers. comm.) the identification of *S. siderea* to Gulf of Guinea and Mozambique remains controversial.

important role in dispersion and settlement patterns, the ocean currents being largely responsible for determining the distributional ranges of coral species (Veron 2000). Despite any contradictory generalization, the correlation among these events provides alternative explanations for a possible long-term transport of eurythermic and sediment-resistant Caribbean coral larvae to the South Atlantic.

Reinsuring great relevance of institutional scientific collections for taxonomy and knowledge of biodiversity, the occurrence of Caribbean siderastreids along the Brazilian coast is supported by the testimony of Hartt's specimen of *S. siderea*. Given the necessity for meticulous examination of skeletal traits to differentiate *S. siderea* and *S. stellata*, it is clear that field identification will always remain speculative. Besides a detailed analysis of septal patterns, which should constitute the basis for *Siderastrea* species separation, additional information on reproductive biology and ecological constraints strengthen the robustness of the decision.

Finally, beyond establishing the occurence of *S. siderea* in Brazil, our study suggests that this species should have been previously misidentified with morphs of the endemic *S. stellata*, which was so far thought to be the only *Siderastrea* species to be found in Brazil. Considering the historical and ecological context, further investigations, including broader collections and field analyses are expected to define the geographic distribution and habitat preferences of *S. siderea* along the Brazilian coast, possibly improving our knowledge on coral dispersional strategies along western South Atlantic.

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